The Veliger 50(4):326–328 (December 16, 2008)

THE VELIGER

Drilling Localization on Bivalve Prey by *Octopus rubescens* Berry, 1953 (Cephalopoda: Octopodidae)

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One Sentence Abstract. An examination of 171 shells of clams (*Venerupis philippinarum* (Adams & Reeve, 1850)) eaten by *Octopus rubescens* Berry, 1953 showed that holes in them were drilled by the octopuses preferentially (64.3%) in adductor muscle scar areas (anterior or posterior), which together comprised only 6% of the total shell area.

Key Words: octopus, drill holes, bivalves, adductor muscles.

Octopuses are well-known generalist predators (Hanlon & Messenger, 1996), but within this generalist approach they also display individual dietary preferences (Anderson & Mather, 2007) and feeding methods (Dodge & Scheel, 1999). Bivalves make up a substantial part of the diet of many octopuses and the methods octopuses use when drilling them, while time-consuming (Steer & Semmens, 2003), are not well-documented and appear to be highly variable (Anderson & Mather, 2007). After drilling, octopuses inject venom into clam prey in order to paralyze the muscle (Nixon & Maconnachie, 1988). Such energy expenditure in drilling might be minimized by selection of particular locations on the bivalve shell (Steer & Semmens, 2003). Anderson & Mather (2007) reported that *Enteroctopus dofleini* drills clams in the center of the shell. This is unlike *O. vulgaris*, which drills around the edge (Ambrose & Nelson, 1983), and *O. dierythraeus* Norman, 1993, *O. minus* Gould, 1852 or *O. bimaculoides* Pickford & MacConnaughey, 1949, which drill over the adductor muscles (Steer & Semmens, 2003; Cortez, et al., 1998; Casey, 1999, respectively).

This inter-specific variation in drilling behavior highlights the fact that one of the central problems octopuses face when feeding on bivalves, in addition to choice of prey, is where to drill on a clam's shell, as different areas of the shell may be thicker or thinner and vital organs of the clam are located in species-specific areas (Kozloff, 1990). Observations of clams eaten by *O. rubescens* at the Seattle Aquarium indicated that individuals may learn to drill clams in particular locations (Anderson, et al., in prep.), while drilling efficiency appears to deteriorate during senescence (Anderson et al., 2008). Despite these observations on potential life-stage specific differences, there are no detailed studies of the localization of drill holes by mature *O. rubescens*, and that is the subject of this report.

Ten *Octopus rubescens* (mean weight: 73.2 g; SD = 64.6) caught in the wild were held at the Seattle Aquarium and fed only Manila clams (*Venerupis philippinarum*, (Adams & Reeve, 1850)) obtained from a local fish market. At least ten shells from clams that had been drilled and eaten were then collected from each octopus over a period of a month (n = 171; an additional 187 were eaten but undrilled). All drilled shells had one hole in them. The holes were typically 1.4 mm wide on the surface (n = 30; SD = 0.28) and 0.4 mm wide on the inner surface of the shell (n = 30; SD = 0.15) as measured with a light microscope. The dimensions of the eaten shells and their adductor muscle scars were also measured and their areas calculated ($\pi \times L \times W/2$).

Locations of drill holes in shells were classified as occurring in the umbo, center, posterior, anterior, or ventral regions of a shell, by the methods of Anderson & Mather (2007) (see Figure 1) and further, whether they occurred within an adductor muscle scar. The mean shell length was 36.2 mm (SD = 4.57). The mean area of the anterior adductor muscle was 2.6% of the shell area and the posterior muscle scar was 3.7% (n = 171).

We used a replicated test of goodness-of-fit (Sokal & Rohlf, 1995) to determine whether proportions of drill hole location (umbo, center, posterior, anterior, or ventral) differed significantly from 20:20:20:20:20. A significant result in the first analysis would indicate *non*-random targeting of particular areas of the shells. We again used a replicated goodness-of-fit test to

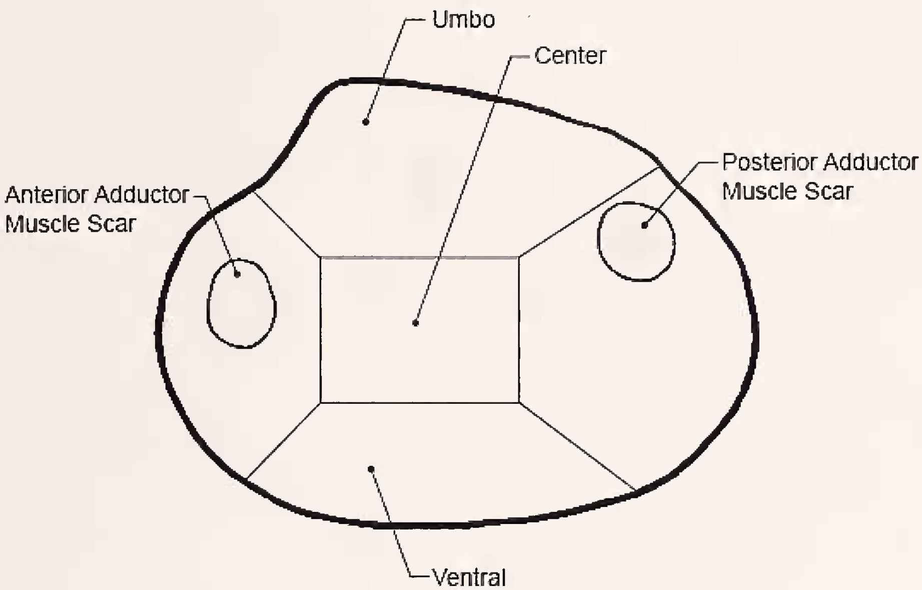

Figure 1. Typical clam shell (*Venerupis philippinarum*) drilled by *Octopus rubescens*. The mean shell length was 36.2 mm. The mean area of the anterior adductor muscle was 2.6% that of the whole and the posterior muscle scar was 3.7% (n = 171). The areas are stylized but are roughly equal in area.

determine whether drill hole location (over adductor muscles or outside adductor muscles) differed from the expected frequency of 6:94. A significant result in the second analyses would indicate that octopuses were actively targeting adductor muscles. Since octopuses could contribute to more than one observation in both analyses we first tested whether the outcomes of all the octopuses were homogeneous (i.e., heterogeneity G-test), that is, were individuals uniform with respect to frequencies of drill holes in the different regions of shell. After taking this octopus individuality into account, we then tested whether the sample as a whole fit the expected ratio of frequencies (i.e., results were pooled within each octopus: total G test). This approach allowed us to examine both individual-level as well as overall average pattern of drilling localization.

Two of 10 individual octopuses drilled with equal probability in each of the five valve locations (heterogeneity G-test = 100.85, df = 36, $P < 0.05$) but overall, there was still a clear significant preference for octopuses to drill in anterior regions of the clams (total G-test = 213.35, df = 40, $P < 0.05$). It was also clear that octopuses were targeting the adductor muscle scars: 64.3% of drill holes were in adductor muscle scars (anterior or posterior), which together comprised only 6% of the shell area. Once again, while some individuals did not drill over muscles as frequently as others (heterogeneity G-test = 40.15, df = 8, $P < 0.05$), there was still a strong significant overall trend for octopuses to drill within muscle scar areas (total G-test = 445.78, df = 10, $P < 0.001$).

Although there are slight differences between external features of the anterior and posterior ends of *Venerupis philippinarum* (e.g., the anterior end is very slightly pointed and the posterior end is rounded, see: Coan et al., 2000), it is interesting to note that the majority of octopus drill holes were located in the anterior end (52% of all observed drill holes, 20% expected by chance alone) and that most individuals appeared to target the adductor muscles. *Octopus rubescens* is known for its potent venom (Hanlon & Messenger, 1996) so targeting adductor muscles which hold the clam shells closed (Kozloff, 1990) for venom injection and paralyzing one of the adductor muscles

Table 1

Frequencies of drill hole locations found in different regions of clam shells left after predation by *Octopus rubescens* (n = 171).

	Anterior	Posterior	Umbo	Center	Ventral	Within muscle scar
Total N	89	24	34	18	5	110
Percentage	52.0	14.0	20.5	10.5	2.9	64.3

may be the most efficient means of accessing food. Cortez et al. (1998) hypothesize there may a direct effect on the nervous system of the clam by injecting venom in any anterior region of the clam. This brings up the interesting question of what features (physical and/or chemical) of clam shells octopuses use to gather information regarding internal location of clam organs and musculature. Given that half of the clams eaten during our study were not drilled at all, are these same cues used to determine whether to drill at all? Clearly, further studies are needed to ascertain the conditions which favor *non*-random drilling behavior in octopuses, including the apparent efficiency of octopuses at drilling shells from clam species with short co-existence histories and the maintenance of behavioral individuality and foraging strategies witnessed here and in other studies (Mather & Anderson, 1993; Sinn et al., 2001).

Acknowledgments. We thank Richard Peters and Paul Blacklow for helpful suggestions regarding data analysis and Barry Shuman prepared the figure. Greg Dietl and two anonymous reviewers provided constructive comments to earlier drafts of the manuscript.

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